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ECOLOGICAL SUCCESSION OF MOSSES

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 266

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(WITH TWO FIGURES)

The work on which the present study in moss succession is based has been confined, with the exception of that done at Mount Carroll, Illinois, to what may be termed the Chicago region. This includes localities showing the typical plant associations within about 40 miles of the city of Chicago. Since the deep rock canyon type of topography is entirely absent in this region, a study has been made of the Carroll Creek canyon, east and west of the town of Mount Carroll, which lies in nearly the same latitude as Chicago and about 125 miles west. The work was begun during the summer of 1916 and continued through the years of 1917 and 1918.

The nomenclature for the plant associations here employed is largely that used by COWLES (3) in his ecological work carried on about Chicago and other localities. Some of these terms may be traced back to WARMING (13), or perhaps farther. The first botanist to make use of this classification by which WARMING divided all plants into xerophytes, mesophytes, and hydrophytes in connection with bryophytes was WARNSTORF (14). Since that time EVANS and NICHOLS (5) have employed these terms in describing the mosses of Connecticut. The terms hydrarch and xerarch were employed by COOPER (2), and are here given the same meaning. The terminology for the classification of the moss species has

been confined wherever possible to that given by GROUT (7). The writer is under great obligation for the verification of all species and the entire classification of many to Mrs. ELIZABETH BRITTON, of the New York Botanical Gardens, Mr. GEORGE B. KAISER, curator of the Sullivant Moss Society, and Dr. LEROY ANDREWS, of Cornell University, and for many suggestions and other valuable assistance to Dr. HENRY C. COWLES and Dr. GEORGE D. FULLER, of the University of Chicago.

Description of region

The city of Chicago occupies a part of the land once covered by Lake Chicago (9). This was a post-glacial body of water formed in the depression between the Valparaiso moraine and the edge of the retreating ice sheet as it slowly moved northward. That the water remained comparatively stationary at certain levels for a considerable length of time after the recession first began, is proved by the presence of at least three distinctly defined old lake beaches. The Glenwood beach marks the edge of the Valparaiso moraine, and is the beach first formed by the impounded water; the Calumet beach was formed at a later period when the water was about 20 ft. lower than at the Glenwood stage; the third or Tolleston beach records a period when the water had receded until it was 20 ft. below that of the Calumet. The beach of the present lake is not far from 20 ft. lower than the level of the Tolleston stage of Lake Chicago, making the surface approximately 60 ft. below that of the original body of water. Going northward along the west shore of Lake Michigan one crosses, in the vicinity of Rogers Park, several old beach ridges of the Tolleston stage. Here the present lake is eroding material deposited by the older body of water. Farther north, about Winnetka and Glencoe, these old beaches have disappeared, and the lake is encroaching upon a bluff of morainic clay, where may be found all stages of clay ravines, from freshly eroded gullies to old ravines in an advanced stage of mesophytism. These ravines have their origin in the small streams which have cut back into the surrounding oak upland. Facing the lake the bluffs are in some places entirely bare of vegetation, while in others they have become well covered

with various species of trees and shrubs, such as *Thuja occidentalis*, *Juniperus communis*, and *Shepherdia canadensis*. On such stabilized bluffs, as well as in the mesophytic ravines, mosses form a conspicuous part of the ground flora. At other points north of Glencoe old dune formations are being eroded. The dune associations, however, are much better shown at the south end of the lake, so that no study of mosses on dune sand has been made along the west shore.

At the south end of Lake Michigan is an extensive sand dune formation reaching southward for some distance. The finer particles of the material eroded on the west shore are carried by the water currents toward the south and there washed up on the beach. The prevailing winds blowing from the lake catch up this fine sand as it becomes dry and carry it farther inland, thus continuing year after year the process of dune building (3). At almost any point which has been left undisturbed by man may be found all stages, from the bare foredune, through the series of cottonwood, pine, early oak, and the well established mixed oak dune formations. At Miller, Indiana, where a part of this work was carried on, the pine dunes are especially well illustrated to the south and east of the Grand Calumet River. This stream, which rises in eastern Indiana and flows almost directly west as the Little Calumet, makes an abrupt curve south of Calumet Lake. It formerly flowed eastward as the Grand Calumet, in a course nearly parallel with that of the Little Calumet, to its outlet into Lake Michigan north of Miller. Later, sand dunes began to form across the mouth, and the stream, being extremely sluggish, was not able to remove the accumulating deposit and was forced to find a new outlet, its present mouth near South Chicago, thus following the path of least resistance. The Grand Calumet now remains as a nearly stagnant body of water which is rapidly filling up with typical pond vegetation. The dune slopes south and east of this part of the river form one of the best moss habitats to be found in the dune complex. Much of the natural flora near the lake and along both banks of the river is being destroyed by the building of cottages. The level of the water in the Calumet has been raised by a dam recently built across the stream farther west. This has not only flooded the low

marshy land near the old outlet and many of the pine pannes north of the river west of Miller, but has submerged the lower part of a transition oak-pine slope south of the river where a special study of mosses had been begun in 1916–1917. Another similar, but perhaps somewhat more mesophytic, habitat is found near Tremont, Indiana, several miles east of Miller on a slope approximately at the same distance from the lake, and south of a smaller stream, Dune Creek, which also flows nearly west for some distance and here empties into Lake Michigan. This also shows a transition from the conifer to the deciduous type of trees, but contains some more mesophytic species, such as *Liriodendron Tulipifera* and *Acer saccharum*, not found at Miller. Mosses are even more abundant here than on the transition slope along the Calumet.

In addition to the region about Tremont and Miller the dune formations have been studied also at Paul, Pine, Long Lake, and Buffington, all located in Indiana. In all these places the same general conditions are met. Starting at the Lake Michigan beach and going southward may be found, in fairly regular order, first the foredune and cottonwood dune on which there is almost constant shifting of sand, followed by the slightly higher and more nearly established pine dune. This is often succeeded by a transition region of mixed oak and pine which merges into the oak dune proper, so that the oldest of the series and the one farthest from the lake is that of the established mixed oak dune on which *Quercus alba* and *Q. velutina* are dominant. These older dunes lie on the border line between the beech-maple climax region of the eastern United States and the oak-hickory climax which seems to be typical near the Mississippi River. For this reason it is somewhat difficult to determine whether these oak forests belong to the latter climax type, or are subclimax associations which will in time develop into the beech-maple type (3).

South of the dune complex just mentioned is another interesting type of topography very completely described by SHELFORD (10). This is a low swampy area made up of long shallow ponds or lagoons, nearly 100 in number, separated by ridges and extending almost parallel to the present lake shore. These ridges were formed by the building up of barrier beaches along the former

shore line, thus cutting off portions of the lake, which then became lagoons. At one time these ponds drained either into the Calumet River or directly into Lake Michigan. Much of this drainage has been cut off by railroad embankments built across the ridges and lagoons, so that these depressions now exhibit a characteristic pond flora. Some of the ponds have reached the shrub or swamp-forest stage; others are dominated by an almost pure stand of cat-tails or bulrushes; still others, ecologically younger, have a considerable area of open water. The ridges in most cases are covered with oak forests.

In addition to the lagoons, hydrophytic habitats are to be found in various swamps and bogs which lie within the Chicago region, all of which offer excellent conditions for bryophytic development. These may be divided into two main types, those which have developed from deep kettle lakes and those which have been formed from shallow lakes or ponds. The former type is illustrated by the bogs at Mineral Springs and Hillside, Indiana; while the latter is represented by the swamp forests at Thornton, Illinois, and Furnessville and Wilhelm, Indiana. The Mineral Springs bog has been developed by marginal encroachment of vegetation on the bottom and by formation of a surface mat in which *Decodon verticillatus* has played an important part. The progression has passed beyond the open water of floating vegetation stage, and even the early stages of mat formation seem to be somewhat telescoped; but here and there are small areas in which either the cat-tails, the bulrushes, or the sedges are dominant. This fen association merges into the shrub stage in which *Rhus vernix*, *Cephalanthus occidentalis*, and *Alnus incana* are most abundant. Beyond the shrub association is the tree area with *Larix laricina*, where in places the quaking condition is still quite evident. In the drier portions of the forest *Betula lutea*, a tree rare in the vicinity of Chicago, makes its appearance. The Hillside bog seems to have had the shrub stage, which here comes in on a dense growth of *Sphagnum*, continued until the substratum is comparatively dry, the forest stages having been subjected to a much greater retardation than is the case at Mineral Springs. The other swamps mentioned have been produced by marginal

growth of plant life on the bottom only. The Thornton swamp lies directly south of Chicago and between the Valparaiso moraine and the Calumet beach line. The Furnessville swamp is east of Mineral Springs, and at about the same distance from Lake Michigan. Both of these swamps have reached the forest stage of development, although there may be standing water in the depressions in the early part of the season. The third swamp, that at Wilhelm, is ecologically of a more advanced type. There is little standing water at any time, and the trees (oak, beech, and hard maple) indicate the approach of the climax forest.

Nearly all of the other associations under consideration are located on morainic drift, either within the region once occupied by Lake Chicago or on the moraine forming the uplands about its borders. Within the Chicago Lake area this till material has been somewhat worked over by water action, but not to a degree sufficient to entirely destroy its drift character. On the east bank of the Des Plaines River, just below its junction with the Sag, is the town of Lemont, Illinois. Here there is an outcrop of limestone which forms several small rock ravines. An abandoned stone quarry in the vicinity, as well as a stone wall at Palos Park and a quarry at Thornton, offer very similar pioneer rock surface habitats. East of Lemont near Palos Park on the edge of the Valparaiso moraine is an upland oak forest which is probably a subclimax forest. Excellent secondary successions in cut-over oak forest in various stages toward reforestation are found south of Lemont near Joliet. East of Joliet along Hickory Creek near New Lenox are much more mesophytic oak-hickory upland forests. At other places we find climax forests of the beech-maple type. At Smith, Indiana, á few miles east of the Wilhelm swamp forest, and at Otis, Indiana, southeast of Chicago, are primeval woodlands containing beech and hard maple of very large size, placing them without question in the climax area of the eastern United States. Along the Des Plaines River south of the northern boundary of Cook County, near Wheeling, Illinois, are mesophytic forests on uplands in which the presence of *Acer saccharum* indicates a greater degree of mesophytism than is frequently met with so far west in northern Illinois. No *Fagus grandifolia* has been

found in this region; but the maple may herald the coming of the climax forest of beech and maple. Directly east of Wheeling, along the lake shore at Glencoe, the upland forests are dominated by oak, although maple is present in the ravines.

The Carroll Creek canyon is a narrow valley with high and in many places nearly perpendicular walls of limestone. The stream meanders back and forth across the ravine and frequently washes against the rock wall. All successions, from the first pioneer lichens and liverworts to trees with decidedly mesophytic undergrowth, may be found within a short distance of each other. This is by far the best moss habitat which has been included in the present study. Although no evaporation data are available upon this region, it is probable that the excess of humidity over evaporation is greater than in the Chicago region proper; while the absence of dust from factories and smokestacks may also be a factor in favor of more luxuriant moss development.

Plant successions

All the successions studied may be placed in two general groups, xerarch successions and hydrarch successions.

Xerarch successions

Under the xerarch series are included all successions which have developed from or through xerophytic stages even though not xerophytic at the present time. Among the most important of these within the Chicago region are the successions on dune sand.

Sand dune succession.—The lake beach, while not strictly a dune formation, must necessarily be included in the dune series leading back from the lake. Here the sand is constantly being moved, either by the waves or, when dry, by the wind. Even during the summer the waves frequently wash over a space several rods in width; while in winter the effect of water and ice is felt still farther inland. Very few plants are able to gain a hold under such unfavorable conditions. Occasionally a few annual seed plants can be found; and sometimes upon the upper beach seedlings of the cottonwood and willows, as well as a few grasses, begin

a precarious existence. Mosses are entirely absent, no evidence having been found even of early germination stages. In addition to the continual change in the surface there is exposure to high evaporation, another factor very unfavorable to plant life.

The foredunes are a result of the obstruction offered to the sand laden winds by plants or other obstacles. Among the plants which may act as windbreaks are *Populus deltoides*, *Prunus pumila*, *Salix glaucophylla*, and *Salix syrticola;* or grasses, as *Ammophila arenaria* and *Calamovilfa longifolia*. There is no indication that mosses ever form a part of the flora. Exposure to evaporation and danger of smothering by sand are probably nearly or quite as great here as on the beach itself. As we enter the cottonwood dune, which is the first of the dune series characterized by trees, we still find constant shifting of sand. Evaporation, however, because of the shade cast by the trees, is somewhat less than in the earlier association. Gradually the sand increases in height about the trees, which continue to grow by adventitious roots (3). In time deposit of refuse from the cottonwoods and growth of ground flora add to the humus content as well as lead to stabilization of the sand. Occasionally under the larger trees or on the more protected leeward side of the dune a few mosses may win out in the competition and live. The first species to appear are such xerophytic forms as *Ceratodon purpureus*, *Bryum ventricosum*, and *B. caespiticium*. If well sheltered, these mosses may continue on into the *Pinus Banksiana* association; or if exposed by change in direction of wind, may be entirely killed out before the cottonwoods are replaced by pines. In no place on the cottonwood dune does there seem to be any considerable growth of mosses. The species mentioned form only scattered tufts or cushions, although in most cases sporophytes are borne freely. Either germination of spores does not often occur, or the young plants do not survive the unfavorable environment. These species probably do not spread so readily by vegetative growth as do many others.

From the cottonwood to the pine dune we usually find a gradual transition, in which *Pinus Banksiana* begins to appear more and more abundantly until the cottonwoods have been eliminated. At about this time *Pinus Strobus* becomes mixed

with *P. Banksiana* on the more mesophytic slopes, and eventually may form a pure stand. During even the early pine stages we may find a thick undergrowth of *Juniperus communis*, with or without *Arctostaphylos Uva-ursi*. These may last until the oaks begin to encroach upon the pines. Both the juniper and the pines produce a dense shade throughout the year, and by shedding needles form a layer of slowly decaying débris. Under the juniper, particularly on north facing slopes, we find the most abundant moss growth of the dune series. Beyond the juniper, where *Arctostaphylos* is very thick, mosses may be present but are less continuous. The bearberry is a plant of low trailing habit, and has the effect of shutting out the relatively small amount of light which penetrates through the dense covering of conifers, and renders photosynthesis on the part of the mosses difficult. The most abundant species of moss under the juniper is *Thuidium delicatulum*, ordinarily considered very mesophytic. Here it forms a thick continuous mat frequently excluding all seed plants as well as most other moss species, and extending beyond the juniper in many places. In this moss mat is a much smaller quantity of *T. recognitum*, not mixed with the *T. delicatulum* but growing in similar places and forming small but distinct portions of the mat. A still smaller amount of *T. abietinum* appears occasionally. Scattered through the *Thuidium* in very small quantities are two other mesophytic species, *Hylocomium triquetrum* found at Paul, and *Calliergon Schreberi* found at Miller. Both species are common in the mesophytic forests farther north (2). About 15 other species of mosses occur upon the pine dune. Some of these are found occasionally under the juniper, but more often on the sand in open places free from juniper, around the bases of trees, or on half-decayed sticks. The most common of these are *Ceratodon purpureus*, *Dicranum scoparium*, and *Funaria hygrometrica*, all of which are species of fairly varied habitat. Much the same condition has been found in all of the pine dunes studied. The mosses are most abundant in total quantity and are most luxuriant on north facing slopes, which in this region are also lakeward facing slopes. A greater number of species occur here than elsewhere in the dunes, unless it is in the transition oak-pine regions, where many

of these species continue on as relics while new ones make their appearance.

Just west of the pine dunes at Miller and south of the Grand Calumet is such a transition region of mixed pine and oak. Along the slope near the river is an abundant growth of mosses, but nowhere except close to the water do they form as complete a covering as in the pine association. Toward the top of the slope they become scattered, and there is also a decrease in the number of species. *Thuidium delicatulum* continues on the lower slope with some *T. recognitum*. Other types found among the conifers are mixed with new species, one of the most common of which is *Fissidens cristatus*. Other forms, either new or now much more abundant, are *Mnium cuspidatum*, *Thelia Lescurii*, *Anomodon rostratus*, *Climacium americanum*, and *Rhodobryum roseum*.

As mentioned previously, another ecologically more advanced transition slope occurs south of Dune Creek near Tremont, Indiana. Conditions here are even more favorable for mosses than at Miller. The presence of such trees as tulip and hard maple before the pines are entirely gone would indicate a telescoping of the oak stages and the rapid advance of the climax forest. The same relative difference in scattered moss patches on the upper slope and almost continuous mat near the base is noticeable here as at Miller. The most conspicuous species is *Aulacomnium heterostichum*, bearing numerous sporophytes. Other mesophytic species not mentioned before are *Bartramia pomiformis*, *Catharinea undulata*, and *Dicranella heteromalla*. *Anomodon attenuatus* occurs in dry situations, usually on tree bases. As already mentioned, both of these transition slopes are near the lake, north facing and south of streams. In striking contrast to these are transition slopes directly south of the pine dunes, farther from the lake, and not in close proximity to streams. Here we see a rapid thinning out of the moss flora. The more mesophytic species disappear entirely and only a few new forms come in. These resemble the types found at the xerophytic tops of the more mesophytic transition slopes.

In the early stages of the oak dune proper, either farther west along the Calumet or south of the pine dunes at Miller as well as at Paul and Furnessville, the mosses are still scattered. In

ravines, however, on slopes with a northern exposure or otherwise protected from desiccation, certain species may be fairly frequent. *Thelia Lescurii*, a gray-green moss growing in loose mats, is dominant and sometimes covers areas of several square feet. *Anomodon rostratus* also appears frequently, and *A. attenuatus* occasionally. *Climacium americanum* and *Rhodobryum roseum* may be found in sheltered spots but not in large quantities. *Ceratodon purpureus* is characteristic in open, less shaded places, while *Catharinea undulata* occurs here and there. A thick continuous moss carpet is never found among the oaks as in the pine

TABLE I

PRESENCE OF MOSS SPECIES IN ASSOCIATIONS OF SAND DUNE SUCCESSION

Species	Cottonwood	Pine	Transition pine-oak	Oak	Beech-maple
Anomodon rostratus	.....	P	P	P	.....
Bryum ventricosum	P	P	.....	.....	.....
Bryum caespiticium	P	P	.....	.....	.....
Catharinea undulata	.....	P	P	P	P
Ceratodon purpureus	P	P	P	P	.....
Climacium americanum	.....	P	P	P	.....
Fissidens cristatus	.....	P	P	P	.....
Funaria hygrometrica	.....	P	P	P	.....
Leucobryum glaucum	.....	P	P	P	.....
Mnium cuspidatum	.....	P	P	P	.....
Rhodobryum roseum	.....	.....	P	P	.....
Thuidium delicatulum	.....	P	P	P	.....
Thuidium recognitum	.....	P	P	P	.....
Thuidium abietinum	.....	P	P	.....	.....
Thelia Lescurii	.....	.....	P	P	.....

dune. As we go still farther south into the later stages of the oak associations, the moss flora becomes less, until about the only species left are *Thelia Lescurii* and *Catharinea undulata* in shaded places, with *Ceratodon purpureus* and rarely *Bryum argenteum* where the sand is more exposed. In forests where white oak is dominant and the forest floor is free from fallen trees, as is the case in many oak forests in this region, *Catharinea undulata* is usually the only moss species to survive. Table I shows the succession of mosses as they have been found in the xerarch series of the sand dunes. P indicates presence of species. Only the species which occur in two or more associations are included.

Why is it that we find this great variation in the moss flora within such a relatively small area as that included within this dune complex? There seem to be at least three causal factors which are worthy of special consideration. First is the constant transportation of sand; second, the exposure to high evaporation; third, and in this case of least importance, competition with other plants. Mosses, because of their low growing habits, are not able to endure covering. Even with such a genus as *Sphagnum*, which is able to continue upward growth year after year, and which has tall erect stems, it is not unlikely that a deposit of sand or sediment would entirely destroy its power of regeneration. There is much less probability that other species which do not have this advantageous habit could contend successfully against covering. Numerous places occur within this region where, through rejuvenation of some dune area, the sand is being carried over more or less mesophytic regions. North of the Grand Calumet near Miller are dunes which have reached the pine stage and which contain many of the species of moss found in the pine dunes south or east of the river. Recent changes, largely due to man, have brought about rejuvenation of the dunes to the windward. The mosses are now in many places early destroyed by smothering, because of the fine sand accumulating about them, and the whole slope, once mesophytic, is undergoing a retrograde succession. Thus it seems quite certain that any dynamic condition which will lead to covering will also bring about the death of any mosses already existing, as well as preventing the growth of the pioneer species. Contrary to the once common opinion, the soil of the new dune is not dry, except near the surface. The water table is always high, and it is necessary only to remove a thin layer of sand to find moisture, even during dry weather. The exposure to evaporation may be great, and this without doubt is the leading cause of the xerophytic structures to be found in dune plants, rather than non-availability of the water supply (6). The work of FULLER gives data upon evaporation in the dune associations, secured in this same region north of Miller. The results regarding the difference in the evaporation rate verify in a marked degree the conclusions to be drawn from the location of the xerophytic

and mesophytic types of moss. Stations for the location of the atmometers were selected in the cottonwood, pine, and oak associations near Miller, and for the beech-maple association at Otis, Indiana. The last, however, is upon morainal clay and not on dune sand. It is not necessary to enter into a detailed account of these results. Fig. 1, taken from FULLER'S work, shows the average of the mean daily evaporation rates in these associations for the three seasons 1910, 1911, and 1912. Fig. 2 indicates the curves for the average of the mean daily evaporation rates in the four associations for the growing seasons of these years.

The absence of mosses on the beach and the foredune is due to the continual change in the surface material and the exposure

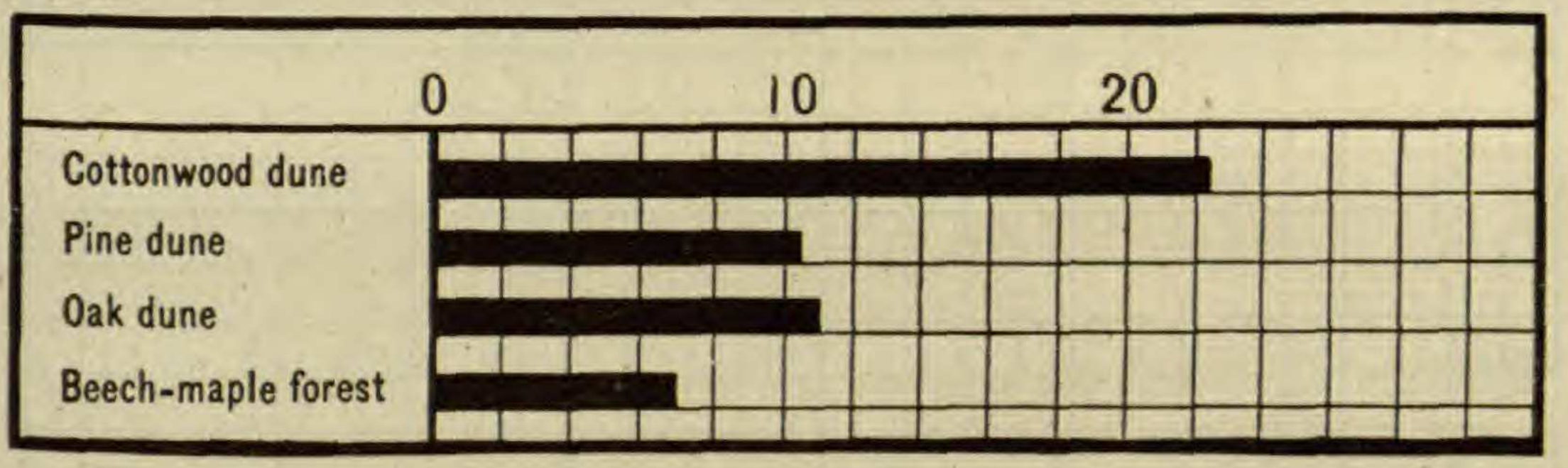

FIG. 1.—Average of mean daily evaporation rates for the 4 associations for seasons 1910, 1911, 1912.

to evaporation. Competition with other plants does not enter into the question. There is not the struggle with wave action on the foredune as on the beach, but there is still constant movement of sand by winds. The plants forming the nucleus of the foredune cast little shade, so that both desiccation by sun and wind and the probability of being covered by sand are as great as on the beach below. The cottonwood dune is higher, the trees afford much more shade, humus begins to accumulate, and as the dune tends toward stabilization there may be much greater protection from wind on the leeward side. However, even on a moderately windy day fine sand is deposited over the ground vegetation so that there is still the struggle to overcome the tendency to covering, and for opportunity for photosynthetic work on which the life of the mosses depends. Evaporation by exposure to bright sunlight and strong winds, while still high, may be somewhat less than on

the foredune. All of these causes tend to exclude any but the most hardy species, and even these are never abundant. The

FIG. 2.—Average of mean daily evaporation rates in the 4 associations for growing seasons 1910, 1911, 1912.

struggle with other plants is not important, since there are always many unoccupied places, and the supply of available moisture is plentiful.

In the pine dune there is a much greater difference in the effect of the first two factors, moving sand and evaporation. It is here and in the mesophytic transition regions that the third factor enters into the causal conditions. According to the results of the evaporation work done by FULLER, the pine dune shows the lowest evaporation rate to be found among the tree associations of the dune series, other than the climax forest. It is still more significant that the rate is lower during the early summer and late fall, the most vital part of the season for mosses. The débris upon the ground aids in the absorption of moisture during rains. The moisture as it slowly escapes from the soil is confined near the surface by the close canopy of the juniper, and also by the dense overhead covering of pines. All of this leads to a high degree of humidity during spring and autumn, the seasons of greatest rainfall, not found elsewhere in the dune associations. In midsummer evaporation may surpass that of the oak dune (fig. 2), but the mosses by that time have passed their period of vegetative growth, and in many cases the production of sporophytes also. The maturing of sporophytes in other species, such as *Thuidium*, is carried on late in the season when humidity again rises. The fact that we find *T. delicatulum* as the dominant species under the juniper indicates decidedly mesophytic conditions, for except as a relic this species usually occurs only in moist habitats. Another reason for its dominance seems to be its ability to endure shade. Either there is no competition with other plants under the juniper or such plants have been crowded out, while *Thuidium* thrives best when well shaded. Other plants become competitive beyond the juniper where herbaceous vegetation, including several typically northern species, becomes more frequent. *Thuidium* less often covers extensive areas, and seed plants may even be found germinating on the mosses. In places more favored by light the mosses are likely to lose out altogether or be forced to take refuge on sticks or bases of trees. Another factor which seems worthy of consideration is that *Thuidium* grows directly on the slightly decayed needles of the conifers. These probably produce a chemical condition of the soil which effectively eliminates many other plants. While the pines also shed their needles, there is much

less material of this kind where the juniper is absent. The competition with shifting sand is nearly absent unless the dune is being rejuvenated. The deposit is so slight that it does not seem to retard either the germination of spores or spread by vegetative growth.

The two mesophytic transition regions from conifer to oak offer nearly as favorable moss habitats as do the pine slopes. Many of the species are relics from the more shaded former conditions, but which now are losing out, largely it would appear by encroachment of other light tolerant mosses, rather than because of competition with herbaceous plants. The shade is much less, especially during late fall and early spring. Many of the mosses are scarcely evident during midsummer. Most of them produce many sporophytes and mature the spores early in the year. That the relative humidity is at times increased by nearness to the water was quite evident on several trips to Miller when the weather previously had been warm enough to raise the temperature of the water of the Calumet. A strong cool wind from the north carried the mist, which was ascending from the river, directly over the transition slope. It was not learned how frequently this happens, but a considerable amount of moisture must be deposited during even a few hours of such a mist. This difference in humidity and water supply is probably one of the chief causes of variation in the luxuriance of the mosses on these slopes and on those farther from the lake, and not in the vicinity of other bodies of water. The evaporation rate at other times is very likely higher than on the pine dune, but unfortunately there are no data for evaporation on these transition slopes. Neither competition with other plants nor movement of sand is a very important factor, unless it may be the latter near the top of the slope.

On the oak dunes we again have an evaporation rate higher than that of the pine dune, except in midsummer. The sparse undergrowth in many places gives little protection from the hot sun which penetrates through the foliage of the oaks. During the spring and fall there is great exposure to somewhat desiccating winds. On many of the more mesophytic northward slopes where mosses might be expected there is often a dense growth of vernal herbaceous plants which seem to have crowded

out the mosses, until the latter are found only on decayed sticks or bases of trees. A few relics from the pine association occur here and there. On some slopes and in ravines where herbaceous forms have not taken full possession, mosses are more common. As previously mentioned, these are somewhat xerophytic species which appeared only rarely in the earlier succession, together with some relics from the former association. It is possible that the roots of the herbaceous plants, because of the need for moisture, rob the surface soil of its water and thus make it more difficult for mosses to secure a sufficient supply. Competition, therefore, can be said to be the great limiting factor on the more mesophytic slopes; while low humidity and high evaporation seem to be more important on those facing the south, where neither mosses nor herbaceous plants are very abundant. Sand laden winds are not of much importance unless the area is near a rejuvenating dune. In the older stages of the oak succession the forest becomes more mesophytic. There is less evaporation and higher humidity, with entire lack of covering by sand. Humus has now accumulated to a degree necessary for the growth of many more species of seed plants. Apparently these have become so successful as to cause almost total elimination of the mosses, which have contributed to their own extinction by adding to the humus content. Only in exposed paths or roads, on decaying logs, or sometimes on tree bases, do the mosses continue to exist at all. Old logs are rare in these woods, and only bases of old trees are favorable habitats, so that in the advanced oak association in this region the moss flora is often almost confined to a few species which spring up in paths or tracks left by the feet of animals.

We may summarize the causal factors for presence or absence of mosses in the dune succession as follows. Mosses are excluded from the flora of the beach and foredune by great exposure to desiccation and to covering by sand. Xerophytic species may appear on the cottonwood dune, but are prevented from becoming conspicuous by these same two factors. Mosses suddenly become abundant in the pine dunes, their growth being favored by high humidity and low evaporation during spring and fall, a result largely of the shade cast by the pines and juniper. Competition

with other plants begins, but is not of great importance; while that with shifting sand has nearly ceased. Whether the moss flora of the transition conifer-deciduous regions resembles more nearly that of the former or of the latter type seems to depend chiefly on local conditions, such as adjacent bodies of water and exposure to winds, greater humidity tending to increase the growth of mosses, and a high evaporation rate bringing about their destruction. In the oak dunes the higher evaporation leads to elimination of the relic species, while it may also lead to the appearance of new xerophytic types. Competition with other plants, especially vernal herbs, becomes a deciding factor, while that of moving sand may be omitted from consideration.

MORAINAL CLAY SUCCESSIONS.—The early stages of moss succession on morainic drift were studied near Glencoe, Illinois. On newly eroded bluffs along Lake Michigan mosses are absent, and in fact do not appear until after other vegetation has begun to take possession and the surface is no longer subject to very active erosion or slumping. On slopes partly covered with *Juniperus communis*, with or without *Thuja occidentalis*, mosses, while conspicuous, do not form a mat of large extent. The species are almost identical with those on sand at Miller. *Anomodon rostratus*, *Thelia Lescurii*, and *Thuidium delicatulum* are the most common. The same similarity on dune sand and morainic clay bluffs has been noted by COWLES (3) for the higher plants. Neither do mosses appear in the early stages of ravines while vertical erosion is active. In later stages, however, they become important and may take no inconsiderable part in stabilization of the surface. Unfortunately it was not possible to study ravines of all degrees of mesophytism, so that the exact period at which mosses appear was not determined. Most of the work was done in ravines having sides of rather gradual slope covered with a subclimax forest and mesophytic undergrowth. A vertical succession, not so evident on the dune slopes, is here a noticeable feature. In one such ravine *Polytrichum commune* is conspicuous among the arbor vitae at the top. Just below this is a good display of *Catharinea undulata*. About midway down the slope is a mixture of mesophytic species such as *Bartramia pomiformis*, *Dicranella heteromalla*, *Anomodon*

rostratus, and *Mnium cuspidatum;* while the lower third of the slope is nearly covered by one hypnaceous species, *Plagiothecium deplanatum*. The entire surface is well supplied with herbaceous undergrowth, but this has not yet been able to supersede the mosses, which, because of absence of decaying woody material, are found almost entirely on the ground. As the ravine widens and enters upon its second period of denudation, more light enters, and the mosses are gradually eliminated by their being a favorable habitat for the germination of seedlings of higher plants which can endure a greater degree of evaporation.

The oak uplands adjoining these ravines are characterized by an extremely impoverished moss flora with the exception of *Catharinea undulata*, which may occur frequently. This is almost equally true of the oak-hickory morainal forests at Joliet, New Lenox, and Palos Park. *Catharinea undulata* is present in all, *Physcomitrium turbinatum* occurs along paths, and at Palos Park *Leucobryum glaucum* is an occasional species. At Wheeling, Illinois, just west of Glencoe on the Des Plaines River, are upland morainal forests which are much more mesophytic than those just mentioned. Of these we may make two general divisions: those which have been pastured so that there are few shrubs and the herbaceous growth is almost confined to grasses, and those which have a mesophytic undergrowth both shrubby and herbaceous. In the unpastured woods, as a marked contrast with the other oak woods just mentioned, mesophytic mosses are common both on logs and on the ground. Among these are *Thuidium delicatulum*, *Mnium cuspidatum*, *Catharinea undulata*, and *Climacium americanum*. In the more open woods which have been partly cut over and subject to grazing, these same species continue on as relics, but are less abundant than before. With these may be *Leucobryum glaucum*, *Dicranum scoparium*, *Polytrichum commune*, and *Ceratodon purpureus*. It is not unusual to see rather large areas given over to *Leucobryum* and *Dicranum* alone or mixed with *Polytrichum*, *Catharinea*, and *Thuidium*. Close to the river, however, along the well drained bluff, we once more find only *Catharinea* on mounds and *Physcomitrium* with sometimes *Funaria hygrometrica* along paths and in tracks.

What is probably the ultimate forest of the region and the climax of the morainic series, the beech-maple type, is seen at Otis and Smith, Indiana. No mosses except *Catharinea* have been found in these forests in any place except on decayed wood or in water holes. In ravines in the Otis woods where humidity is higher (figs. 1, 2) mosses are a little more common, not growing on the ground, but on sticks, stumps, or bases of trees. These are almost invariably some species of Hypnaceae.

Of the three leading causal factors mentioned for the sand association, water erosion may be substituted for wind erosion and covering. As long as very active denudation continues on a lake bluff or ravine slope, resulting either in a gradual wearing down of the surface or in slumping, mosses have no chance to become established. While evaporation on the bare slope may be excessive, neither that nor competition with other plants is the primary factor. In the later stages, however, these become the two determining conditions. Wherever the arbor vitae and juniper are present we have a repetition of approximately the same conditions as under the pines and juniper on the dunes. The arbor vitae is near its southern limit at Glencoe and does not form a thick cover, and for this reason has less influence as a shade producer than has the pine. On the other hand, the juniper may be just as dense and as effective in producing shade and in retaining moisture as in the former situation.

ULRICH (12) has made a study similar to that by FULLER in the ravines at Glencoe. Three stations were used which correspond roughly to the three elevations on the ravine slope just described, and the results justify the supposition that evaporation is the main cause of such a difference. The station near the top in what would correspond to the *Polytrichum* area showed the highest rate of evaporation; that on the middle of the slope or the region of mixed mesophytic mosses gave a lower rate; that at the bottom or the area of Hypnaceae gave a still lower rate during a part of the season, although at times it was slightly in excess of that midway up the slope. This is exactly what we would expect from the nature of the species present and a comparison of the conditions in other regions where they are found. Competition with other

plants is no doubt an important factor on many such slopes, as they offer conditions increasingly favorable to other ground flora. Erosion decreases in importance as a determining factor in proportion as the mesophytism increases. When the ravine reaches its second denudation period, accompanied by greater sunlight and evaporation, the mesophytic mosses are eliminated along with the other mesophytic undergrowth; but these may reappear when the slope has once more attained a relatively permanent condition, and continue on until the climax association is reached, or may even persist into this association if logs and stumps are present.

In the open oak forests the moisture supply in air and soil probably is again largely the controlling condition, as in the oak forests on dune sand. Other plants do not occupy the ground to so great an extent as to exclude mosses because of lack of space alone, and there is little probability that the mosses would become shaded to a sufficient degree to shut out the light and prevent the necessary photosynthetic work. Just why there is so great a scarcity of mosses in the more mesophytic oak or oak-hickory forests, as well as in the beech-maple climax, both of which provide relatively high humidity and low evaporation rate (**6**), has not been fully determined. Competition with other plants may be accountable to a great extent, but even this does not seem sufficient to cause the almost complete elimination of mosses from these forests. In some places there is a continuous succession of dense ground vegetation during most of the growing season, which might be able to prevent the development of mosses; but in other places the vernal flora does not seem to be followed by a conspicuous aestival flora, yet mosses are not present. Perhaps the competition with the vernal flora in its prime, when most mosses attain their greatest growth, may be sufficient to prevent both spore germination and vegetative growth at this time, so that presence or absence of ground vegetation later in the year is of little consequence. The fact that when old logs are present, mosses are common upon them when not found on the ground, would indicate that they had not been able to hold their own against the herbaceous plants. Another factor which may have a

decided influence is that of the chemical change in the soil due to increase of humus. Just what the difference is which seems favorable to the germination of the seedlings of the climax trees and not to those of the former association, and how much of this difference is chemical and how much physical and related to light, are questions for future solution. Whatever it is, it would probably affect mosses as well as other plants. That an acid condition of the substratum alone is not detrimental is indicated by the luxuriant growth of many species on decaying wood and upon needles of conifers.

The great abundance of mosses in the upland oak forests along the Des Plaines River seems to be related to the slightly greater humidity of the atmosphere and larger supply of available soil moisture. There are indications that much of this region has been and still is at certain seasons somewhat swampy, so that there may be some question whether it belongs in the xerarch succession proper or should be placed in the hydrarch swamp series. While the final outcome would be the same in the two series, the intermediate successions would differ to a very large degree. The presence of the relic species in the grazed woods or partially cut-over land seems to be explainable by the fact that they are mosses of wide extremes of habitat, and are highly light tolerant. The change in environment appears to have taken place so gradually that the mosses have been able to become adapted to the greater xerophytism without themselves being materially altered.

The successions on morainic drift may be summed up in a few points. Mosses are entirely absent on the newly eroded bluffs and in the early stages of the ravines. They do not become conspicuous in the ravines until a rather advanced state of mesophytism has been reached, but they probably play an important part in the stabilization of the clay surface and addition of humus, which hasten the advance of the seed plants. Mosses appear in the conifer stage on the bluffs, forming part of the heath mat under the juniper. They are most abundant in the middle aged ravines, before the second xerophytic stage is initiated by the widening of the ravine and decrease of the angle of the slope.

On the oak upland and in most oak and oak-hickory forests of the subclimax type mosses are nearly absent, particularly where decayed logs are not to be found. The same paucity of mosses occurs in the beech-maple climax forests of this region, where competition with other plants or chemical conditions of the soil may be the leading cause. The increase in moss flora along the Des Plaines River at Wheeling seems to be a result of former and present better supply of moisture in soil and atmosphere.

ROCK SUCCESSIONS.—The rock successions are poorly represented in the Chicago region. The early pioneer stages of lichens and mosses, however, can be distinctly traced at Lemont, Illinois, near the Des Plaines River, on rocks of Niagara limestone which have recently been exposed, on the sides of an old stone quarry, on a cliff in an open pasture, and in several small ravines. The early crustose lichens are followed by *Bryum argenteum* and *Grimmia apocarpa*. *Ceratodon purpureus* seems to succeed these or even to appear with them on the flat rock surfaces, either on the top of the cliffs or on the bowlders. Many rocks have been exposed during recent excavations in straightening the channel of the stream. These are frequently well covered with crustose lichens, and the first moss to invade the lichen zone is *Bryum argenteum*, so that in this case at least this species is a pioneer moss. Elsewhere on rocks it seems often to come in later than *Grimmia*. At the mouth of the ravines, wherever the rocks are still exposed to xerophytic conditions, the struggle is going on between the mosses and lichens. The pioneer mosses usually smother out the crustose lichens, but in turn may be covered up by small species of the foliose lichen group. The mosses here never become very abundant, nor do they occupy large spaces. On the vertical faces there are numerous small cracks and pits in the rock which offer a better hold for typical crevice species, such as *Funaria hygrometrica* and *Gymnostomum rupestre*. Crevice forms are somewhat more abundant in the cracks of a stone wall at Palos Park where the mortar has disintegrated. At the quarry near Thornton, where the horizontal surface of the limestone has been denuded, there are numerous patches of *Funaria hygrometrica* and *Ceratodon purpureus*. Within the limits of Chicago, at Stony Island, although

the rocks have been long exposed, only very depauperate specimens of these same species occur. The later stages of the rock succession are absent. All of these places, with the exception of Stony Island, are surrounded by agricultural lands, and whatever has been the natural fate of this series has been too nearly obliterated by man to allow of its determination. At Stony Island the top of the rock is covered with prairie vegetation. The presence of a few oak trees seems to indicate that without the intervention of man the grasses would have been followed by an oak forest. The conditions at Lemont may have been much the same. In the ravines themselves the mosses belong almost without exception to the Hypnaceae and are without sporophytes, and hence are difficult to determine. *Brachythecium digastrum* is a rather common species.

The Carroll Creek ravine, where humidity is much greater and there is considerable seepage of moisture over the rock surface, is a much more favorable habitat for mosses than are the rock outcrops in the Chicago region. The number of species is not large, but those which do occur are plentiful and they form a thick covering over the rocks. Wherever the stream comes in contact with the rocks, and in other very moist places, liverworts are the first plants. Above the liverwort zone, or on rocks less closely in contact with the water, is the zone of crustose lichens. These are usually followed by foliose lichens, although quite often the pioneer mosses may succeed the crustose and contend for possession with the foliose lichens. The first moss is *Grimmia apocarpa*. On rocks in the open, exposed to strong insolation the greater part of the day, this species is abundant both on horizontal and vertical surfaces. Accompanying this is *Bryum argenteum*, which may occur almost if not quite as early, and in even greater quantity, particularly on horizontal surfaces.

This region offers the best illustration of a very definite succession of mosses on mosses. Here a second or even third moss stage is common and may occur on rocks in the open as well as on those in mesophytic shaded places in the ravine. The species which constitute the later stages differ in the two situations. In sunny places *Bryum argenteum* frequently forms the second stage,

with some Hypnaceae as the third vertical layer. An especially good example of this was found on a low rock situated on a hillside in an open pasture, and at some distance from the stream. The top of the rock sloped a little in the downhill direction and was slightly lower than the ground at the upper edge, but was perhaps 2 feet above the ground at the lower side. Numerous bushes overhung the upper border, but the lower part was exposed to full sunlight. On the shaded vertical face was a small quantity of a liverwort and an extensive growth of crustose lichens. The liverwort did not grow over the edge at the top, but the crustose lichens which had spread over much of the upper surface were being overgrown by foliose lichens. Growing among and over these was *Grimmia apocarpa*. Overlying the edge of the *Grimmia* and in many places entirely covering it was *Bryum argenteum*, forming a thick compact mat over a large part of the remainder of the rock, except at the upper side where soil had washed over the surface from the ground in contact with it above. Here *Brachythecium acuminatum*, growing partly on the soil, was extending out over the *Bryum*, forming a third moss layer. Small patches of lichens and of *Grimmia* here and there indicated that these at one time had been pioneer plants over the entire surface. When the two more mesophytic species came in, they had developed more rapidly on the part of the rock which received the most moisture from the ground and which was also somewhat shaded by overhanging bushes.

In shaded places along the creek in the ravine proper several species of *Anomodon* form the moss stage following the pioneers. As would be expected, the change in species occurs more rapidly in spite of the slope of the rock, which more nearly approaches the perpendicular. In some places the cliffs are quite closely covered with *Juniperus virginiana* and deciduous trees and shrubs. Under these and often overhanging the edge of the cliff is an undergrowth of *Taxus canadensis*, reminding one of the *Juniperus communis* under the pines in the dune region, except for the greater mesophytism which is indicated by the herbaceous flora. On vertical rock faces, well shaded and with water dripping over the surface, a luxuriant mass of *Anomodon viticulosus* is the only common

species. On surfaces with a more gentle slope, where the moisture supply is somewhat less but still plentiful, this species, either alone or with *Anomodon rostratus*, forms the second moss stage. Where exposure to evaporation is greater, *Anomodon rostratus* alone, of the two species, occurs. Under the *Taxus* is a close moss carpet in which *Thuidium delicatulum* forms the third moss layer, and the second species is ordinarily *Anomodon rostratus*, which has smothered the *Grimmia* except at a very few points. Other species which help to make up this moss carpet often several inches thick are *Climacium americanum* and *Rhodobryum roseum*. This seems to be a moist habitat even during very dry periods. Another even better successional series was found on a rock on a more gradual slope, well shaded by deciduous trees of an older ecological association, and well above the level of the stream. This rock projected out a short distance from the bank, leaving a small space between the rock and the ground below. On this protected lower surface *Fissidens cristatus* formed a complete covering and in places extended up over the edge of the rock. Growing over this on the upper surface and reaching down over the edge at some points was a thick mat of *Anomodon rostratus*. Upon the *Anomodon* was a third stratum of *Thuidium delicatulum* and a small quantity of *Entodon cladorrhizans*, in all forming a compact mat of considerable depth. No traces remained of the typical pioneer mosses. The lichens showed occasionally under the *Fissidens*. On the *Anomodon* were patches of a powdery lichen and also of a fruticose species, showing that these may develop on the mesophytic mosses. *Climacium* and *Rhodobryum* again formed a small part of the last moss stage. Growing in this carpet of moss were such plants as *Pilea pumila*, *Geranium maculatum*, small ferns, and tree seedlings, indicating that the next succession is to be that of the vascular plants. Many such examples of the vertical succession of mosses are to be found throughout this ravine.

Such a moss carpet has been described by COOPER (2) for the rock surfaces on Isle Royale, and by BRAUN (1) for the conglomerate rocks near Cincinnati, Ohio.

At the top of the perpendicular cliffs there seems to be no special variation in mosses. Backward from the margin the same

pioneer xerophytic species soon give way to the more mesophytic ones. From the edge there is usually a rather abrupt slope upward for a few rods, which is thickly wooded, in most cases with oaks sparsely sprinkled with red cedar, and here and there a white pine. The undergrowth is decidedly mesophytic, and on the rocks are the same mosses already given for the other moist shady habitats. Immediately beyond the strip of wooded land are cultivated fields.

In comparing the sparse moss flora on rocks of the Chicago region with the very luxuriant display along Carroll Creek, where general climatic conditions must differ only slightly, one at once begins to search for the cause of the variation. While the rock exposures around Chicago are not extensive, they are sufficient to serve as a basis of comparison. The rock in both cases is dolomitic limestone, not differing enough in structure to be an important factor. The only outcrop which is near enough to Lake Michigan to be affected by the greater humidity is that of Stony Island, and that is, if anything, more barren than are the other regions. The cliffs and ravines at Lemont are not close to the stream as are those at Mount Carroll, but are on what was probably the river bluff at some past period when the stream contained much more water than at present, in all probability when the Des Plaines River was the outlet of the old Lake Chicago. Now the cliffs are not near any body of water, and in the ravines are only small streams which are nearly dry a part of the year. The stone quarry at Thornton is being worked by a cement factory, so that the exposure, with the exception of the rocks along the top, is too recent to afford any information. The amount of moisture which could come from the pool of water in the bottom of the quarry cannot be great enough to affect the flora on the horizontal rock surfaces above. The quarry at Lemont has been abandoned for some time, and much of the bottom is overgrown with weeds and grasses. The pools of water in the depressions may add slightly to the humidity of the air in the immediate vicinity; while the vegetation growing up from below and that overhanging from the upper edge of the rock undoubtedly adds to shade and contributes to a lower rate of evaporation. The

rocks near the Des Plaines River, thrown out in straightening the channel, have also been exposed for only a short time. It would seem therefore that the recent exposure in some cases and the distance from bodies of water sufficiently large to locally affect the humidity may be two of the reasons for the poor development of rupicole species. Another probably greater factor, at least for Stony Island and Thornton, is the large amount of dust which accumulates on vegetation, very effectually hindering photosynthetic work. At Stony Island there is much fine coal dust from smokestacks and trains, as well as dust from factories. At Thornton a large quantity of fine white dust thrown off from the cement factory accumulates in a thin layer and forms almost a crust, after light rains, on the foliage of all plants. There is less dust at Lemont, where there is a somewhat better development of mosses, but still much more than along Carroll Creek, which is bordered only by forests and farm lands, and is far from any factories. The later stages of succession on the rock outcropping near Chicago, as stated before, have been greatly interfered with by man. Evidently the change from pioneer conditions is extremely slow, and there is no development of true forest, so that all moss stages beyond the pioneer are so far wanting.

Returning once more to the Carroll Creek ravine, in great contrast to the Chicago region there is a narrow valley flanked by steep rock walls upon which direct sunlight falls for only a short number of hours each day. That this has much to do with the lower evaporation and higher humidity is indicated by the more mesophytic undergrowth and the greater luxuriance of mosses on all undisturbed north facing slopes. Whatever moisture enters the air through evaporation from the stream will be carried away slowly, since such a valley is well protected from winds. Another condition which also points to the moisture from the water as an important factor is that the greater growth of mesophytic mosses is found at places where the stream in its meanderings comes close to the rock wall, either on the north or south side of the ravine, and that the mosses are more luxuriant than in other places with a similar exposure but farther from the water. An additional cause may be found in the length of time in which snow

remains upon these north facing slopes. In places sheltered from the warm spring sunlight the snows melt slowly, and the moisture soaks into the humus instead of running off rapidly, as it must do on such an incline when the snow melts more quickly. It is well known that in general the moss flora becomes more conspicuous as we go north into the cold temperate regions. This condition is comparable to that of the northern habitats where much of the snow disappears under the action of sunlight and not of rains. Since these slopes are exposed to a lower degree of insolation even during the summer, the mosses are never subject to extreme desiccation. This cannot be true of the rock habitats which lie within the Chicago region.

The great economic importance of such a moss covering is demonstrated by the growth of seedlings of higher plants upon the moss mat, which leads to the initiation of the tree associations. Herbaceous plants grow to maturity and produce seed on moss covered rocks, with the roots obtaining nutriment only from the decayed moss material. The slower growing tree seedlings can exist in a like manner for several years, by which time their roots may be able to penetrate through the crevices or between the rocks to the soil below. Mosses are very hygroscopic and quickly absorb water during rains, but give it up slowly. Several days after rains water can be pressed from these mosses even though seepage is not an important factor. In addition to this is the immense value of a moss covering on rock slopes to conserve the water supply and prevent flooding of the adjacent land along the lower course of the streams. The great value of mosses in relation to the conservation of moisture and their effect upon the soil was observed by OLTMANNS (8). He says:

> A moss carpet acts as a sponge. A dense low carpet with countless capillary spaces between leaves and rhizoids absorbs capillary and superficial water, but obtains little or none by suction from soil and internal conduction. Consequently living and dead carpets of moss imbibe and evaporate approximately the same amount of water. A carpet of moss does not desiccate the soil . . . . they dry it to a less degree than does other vegetation, and they protect dry easily heated soil from desiccation.

EVANS and NICHOLS (5) also discuss the economic value of mosses in such situations.

The moss successions on rock surfaces may be summarized under two main heads: (1) There are at least four factors which are of special importance in accounting for the better moss development on rocks a long Carroll Creek than in the Chicago region: the greater humidity in the former place because of nearness to a stream and lessened exposure; a lower evaporation rate due largely to the fact that the rocks are sheltered from direct rays of the sun for a greater number of hours each day; the slow evaporation of the large quantity of water taken up by the moss mat during the gradual melting of the snow, and consequent lack of desiccation; and the freedom from atmospheric dust, common about any large city, which tends to retard photosynthesis. (2) Mosses are of special value on a rock substratum, as soil formers, to form a habitat for herbaceous plants, to initiate the early tree associations, to conserve water supply and to prevent floods by too rapid run-off, and to add to the aesthetic beauty of the landscape.

RIVER BLUFF SUCCESSION.—Another somewhat xerophytic habitat is that of a high river bluff as seen at Thornton, Illinois. In this region Thorn Creek, a comparatively small stream, has cut down much below its former level, resulting in drainage of the adjacent land and a consequent lowering of the water table. The trees along the bluff are deciduous and sufficiently scattered to allow penetration of the sun's rays, even during the summer. Because of grazing there is no shrubby undergrowth. Here are such mosses as *Catharinea undulata*, *Leucobryum glaucum*, *Ceratodon purpureus*, *Funaria hygrometrica*, *Polytrichum commune*, and *Physcomitrium turbinatum*, all of which are quite abundant. All of these, except the last, are found in the neighboring swamp forest. *Catharinea*, which is usually found only in the mesophytic forest, is probably a relic from a previous period of greater mesophytism. *Polytrichum*, while often found in rather dry places, seems usually to originate in mesophytic or even swampy habitats, so that it also is likely a relic. *Leucobryum* and *Funaria* have a wide range of habitat, and may be either relics from a more moist condition, or pioneers on soil constantly becoming more xerophytic at the surface. *Ceratodon* and *Physcomitrium* are doubtless sub-

sequent species, as they are found only in somewhat xerophytic species.

We have, therefore, a retrogressive succession indicated by the moss flora, which is a mixture of relic or antecedent, typically mesophytic species and the subsequent xerophytic forms. Such retrograde successions are not uncommon wherever surface conditions of soil water and exposure to evaporation have undergone rather gradual modification.

Hydrarch successions

Under this heading have been included all successions originating in water or very moist habitats, with the exception of the moist rock succession already described.

Floodplain succession.—This succession was studied at several points along the Des Plaines River, as at River Forest, Riverside, on the east bank at Wheeling, and also along Carroll Creek. The work has been of importance only for its negative value in establishing the fact of almost entire absence of mosses in such associations. Late in the season a few immature plants may sometimes be found, but these seem never to reach maturity if growing on soil, although a few well developed sporophytes may be found on plants growing on logs above the high water level. The true floodplain is subject to inundation during spring rains and during high water at any season. A great quantity of fine alluvial sediment is carried over the land and settles to the bottom with the recession of the water, leaving a crustlike layer of variable thickness over the ground and on any vegetation which may be present. The moisture conditions, except during the flood period, are favorable to spore germination; but the frequent deposit of fine material, particularly at the period when the moss plants would begin the season's growth, seems to be sufficient to destroy the ephemeral protonema which by any chance may begin to develop. The immature plants found later in the season probably come from late germination of spores which have escaped destruction or which have reached the floodplain from the surrounding uplands after the spring inundation.

Evaporation on a floodplain is not excessive, and the available supply of soil moisture is high, so that these two conditions

cannot cause the absence of mosses. Competition with the abundant herbaceous flora either in the spring or summer is only a secondary cause, if worthy of consideration at all. If competition were a prime factor, we should find somewhere in the floodplain succession, either in the horizontal series from the water back to the upland or in the series from the standpoint of time from the floodplain formed by the younger stream as it begins deposition, up to the old floodplain of the mature river which has nearly reached base level, an association in which mosses take an important part. This has not been observed on any of the floodplains under consideration. It is not, therefore, a case of being crowded out by other plants, but rather an inability to survive the unfavorable dynamic conditions along a depositing stream, which are as effective in eliminating mosses as was the active erosion of the earlier stages in the stream's development.

SPRING STREAM SUCCESSION.—At Otis, Indiana, and New Lenox, Illinois, are numerous springs, the water of which is highly impregnated with iron compounds. As the water comes in contact with the oxygen of the air, bog iron ore is produced which builds up mounds about the outlets of the springs until the water can no longer force its way to the top for escape, and finds a lower exit where there is less resistance to be overcome. Very frequently numerous species of plants make up a large part of the foundation structure of the tufa. Taking part in this tufa formation is a coarse moss, *Brachythecium rivulare*. The chemical substances in the water penetrate the plant tissues which, as they grow old, resist decay and form a porous rocklike mass. In the larger stream forming the outlet of such springs at New Lenox are several species of *Amblystegium* growing on submerged sticks and stones, but these do not enter into the tufa formation. A few other species, not typically water forms, grow on sticks which emerge from the water.

A somewhat comparable case of the formation of travertine in the waterfalls of the Arbuckle Mountains in Oklahoma has been described by EMIG (4), in which the two mosses *Didymodon tophaceus* and *Philonotis calcare* are the species involved. Still another species, *Cratoneuron filicinum*, has recently been collected by

COWLES at Turkey Run, Indiana, where it is a common species aiding in the tufa formation in the waters of similar mineral springs (11).

POND AND LAKE SUCCESSIONS.—The pond and lake successions may be classed in two general groups based on the ecological development. The early successions are represented in the Chicago region by two subdivisions, the pine pannes examined at Miller and the lagoons of Buffington and Long Lake, Indiana. The later successions may be found in the swamp forests at Wilhelm and Furnessville, Indiana, and Thornton, Illinois, and the bogs at Mineral Springs and Hillside, Indiana.

Early stages of pond succession.—Pine pannes.—The pine pannes are depressions among the dunes, so low that water which seeps through the sand from the lake, or in this case partly from the Grand Calumet River, reaches the surface or even may rise above it. Some of the depressions may be quite dry during the summer; others may have sufficient water to withstand ordinary summer drought, and remain wet throughout the year. Surrounding the more or less circular body of water in the center of the larger depressions is a border of pines of the same species as previously mentioned for the pine dunes. As a general rule we do not find a typical pond flora even in the center, probably because the quantity of water may be subject to great variation during the year. Sedges and marsh grasses are common, especially near the margin. Only one species of moss forms an extensive growth, namely, *Campylium stellatum*. It may be entirely submerged in the shallow water, but seems to thrive equally well along the edge where it emerges, and, as a relic from a former hydrophytic condition, may even be found on the higher ground at the edge of the tree zone. It is not a floating species in the pannes and is not found in deep water, yet it is the same species which forms much of the substratum of the floating islands in the lagoons at Buffington. While it cannot be considered as a tufa former, it aids materially in filling up such depressions. On the higher land among the trees other mosses are either absent or, if present, are of the same species as already given for the early pine dunes.

Lagoons.—The lagoons at Buffington have been described in the first part of this paper. The water is much deeper than in

the pannes, and the vegetation varies from the submerged species in deep water to the forests on the drier ridges. Floating in the deeper lagoons and sometimes emerging in the more shallow ones is a large quantity of *Drepanocladus fluitans*, *D. aduncus*, and *Campylium chrysophyllum*, and perhaps other closely related species. Around the margin of many lagoons are *C. stellatum*, already mentioned for the pine pannes at Miller, and *Bryum ventricosum*, which has also been found at Long Lake and Pine in much the same situations. In the larger lagoons are several floating islands, of which *C. stellatum* forms a large part of the foundation. In the larger lakes about Chicago, such as Wolf and Calumet lakes, the same marginal soil species of moss occur, but so far none has been found floating or submerged in the deeper water.

Wherever mosses appear, either floating or along the margin of ponds, they aid greatly in the conversion of depressions into land by promoting the advance of other terrestrial plants. There seems to be little difference in the mosses of the pannes and lagoons, except that which can be accounted for by the more shallow water in the former, which may subject the plants to seasonal periods of desiccation, and which would prohibit anything in the way of floating mosses or of floating islands. In both cases it is quite evident that mosses are an important class of plants in the early stages of the pond successions.

Late stages of pond or lake succession.—Swamp forests.—When comparatively shallow ponds and lakes pass from the aquatic conditions, the progress toward the later associations is by growth of vegetation upon the bottom along the margin. Waste material accumulates. In time the open water in the center is entirely eliminated, and a swamp results, which, depending on local conditions, may pass into a prairie where mosses take little part, or into a forest where they may be of prime importance. The Thornton and Furnessville swamps are illustrations of the latter type of development in rather early stages, while that at Wilhelm gives a later condition much more mesophytic. The first two are still characterized by depressions and hummocks, which are rarely encountered in the Wilhelm forest. Although humidity, shade,

and other factors of environment do not differ widely in the three areas, only five moss species have so far been found common to all. These are *Ceratodon purpureus*, *Mnium cuspidatum*, and *Catharinea undulata* on higher land or on logs, and *Brachythecium rutabulum* and *Amblystegium radicale* in low wet places. All except the first are mesophytic species. The *Ceratodon* occurs rarely and then on sticks which are in rather dry locations in the open or along the margin of the swamps. *Sphagnum* and *Leucobryum* are found only at Thornton, the former growing on the ground in depressions, and the latter on hummocks. Wilhelm far surpasses the other forests in the total quantity of the moss flora. *Thuidium delicatulum* grows abundantly on decaying logs and occasionally on the ground, and is perhaps the most conspicuous species with the exception of *Mnium cuspidatum*. *Thuidium recognitum* and *Anomodon rostratus* are found in smaller quantities, usually on logs or tree bases. Several of the very mesophytic species, such as *Climacium americanum* and *Rhodobryum roseum*, are common both on logs and on the ground. The shade is dense, and decaying plant material forms a thick layer on the forest floor. The moss display is of greater luxuriance than elsewhere in the Chicago region and is a close rival of that of the Carroll Creek ravine.

Bog forests.—The two bogs studied within the limits of the region under consideration are the tamarack bog of Mineral Springs and the *Sphagnum* bog near Hillside. Several typical associations in the ecological development can be distinguished: the sedge mat, shown at Mineral Springs; the shrub stage, well developed in both bogs; and the tamarack tree association at Mineral Springs. An additional division might be made of the *Sphagnum* moss association at Hillside, but this is a slightly different line of development rather than another ecological association.

As stated before, the bog successions are distinguished in origin from the pond successions, in that they are formed on sedge mats which grow out over the surface of deep lakes, forming quaking bogs, which may remain in a very unstable condition for many years. The first association to be found at Mineral Springs at the present time is a mixture of bulrushes, cat-tails, and

sedges, all of the early aquatic plants having disappeared. Mosses are about equally conspicuous over the whole of the sedge mat, and consist chiefly of six species, all long-stemmed and of somewhat upright habit of growth. They form a rather close packing about the roots of the other plants. All are very hygroscopic and grow partly submerged. The most noticeable is *Calliergon cordifolium*. The others are *Campylium stellatum*, *C. hispidulum*, *Drepanocladus aduncus*, *D. fluitans*, and *Brachythecium rivulare*.

In the shrub association, where the shade is somewhat increased, these species continue, but decrease in quantity. New species do not seem to come in until the late shrub or early tree associations which again show no distinct line of demarcation, but merge into each other. It is here that we get the first development of *Sphagnum* in the Mineral Springs bog. *S. palustre* occurs usually in low wet depressions and has not formed a very extensive growth either among the shrubs or in the tree association where it becomes more abundant.

COOPER (2), in his paper on the mosses of Isle Royale, discusses the presence and absence of *Sphagnum* in bogs. He concludes that *Sphagnum* comes in on the sedge mat following sedges of low growing habits, which produce little shade and offer only slight obstruction to the spread of the moss by vegetative growth. The inference is that *Sphagnum* does not germinate in shade, although it may spread into forests by vegetative growth from outside regions.

This theory does not hold for the swamps and bogs of the Chicago region. In the Mineral Springs bog the most common sedges are relatively large and coarse. At Hillside the early sedge stages are past, but the species still present are all tall and coarse. In the former bog *Sphagnum* does not appear on the sedge mat; in the latter *S. recurvum* has in most places entirely replaced all early associations. At Mineral Springs *S. palustre* begins in the transition shrub-tree area, and becomes most abundant among the tamaracks, where it is frequently found entirely disconnected with any present *Sphagnum* region even in the transition association. There is no evidence that it has spread from a less shaded place of germination on the sedge mat, and there seems to be no explanation of its presence other than that it has been able to

start under the shade of the trees and shrubs. North of the Mineral Springs bog is a low, flat, sandy plain covered with shrubs and marsh grass. The undergrowth is a compact mass of *Sphagnum*. In many old lagoons which have reached the shrub stage or which have a rank growth of swamp grasses, *Sphagnum* is growing in rather dense shade, but whether it originated in shade or sunlight cannot now be determined. Another case which is similar to that of Mineral Springs is the presence of *S. subsecundum* in isolated patches in the depressions of the Thornton swamp. There is no connection whatever with outside *Sphagnum* areas. In fact, no *Sphagnum* has thus far been discovered in the open regions around the swamp. Many of these patches are in the interior of the forest, and all are well shaded during the summer. It is quite true that in both the Mineral Springs bog and the Thornton swamp the trees are bare of foliage during the winter season, and therefore sunlight will reach the ground during the early spring. This argument, however, can be applied equally to the sedge association, where there is little shade from the coarse sedges until the new growth has begun. In this region, therefore, it appears that *Sphagnum* must be able to germinate under shade, and that it may be present in forests without having reached these habitats by vegetative encroachment from outside areas. This conclusion is borne out by work done upon the germination of *Sphagnum* by GEORGE L. BRYAN. The results of the study have not yet been published, and I am indebted to the kindness of W. J. G. LAND of the Botanical Department of the University of Chicago, under whose direction the work was carried on, for permission to refer to the results. BRYAN made many careful experiments upon the germination of *Sphagnum* spores under various conditions of soils and sunlight, and found that germination occurred in all degrees of sunlight and in darkness itself. Apparently there is some other determining factor which controls the presence of this group of mosses.

The tamaracks form a border about the bog. On the outer margin they are being displaced by other bog trees, as *Betula lutea* and *Nyssa sylvatica*. The tamaracks grow on hummocks, while the depressions between them may be very wet or even filled with

standing water. A large number of species of moss which have not been found in the previous bog associations occur here, on the ground, on sticks, or on logs. *Calliergon cordifolium*, the two species of *Campylium*, the *Brachythecium*, and *Drepanocladus aduncus* continue, often on partly submerged sticks. In slightly higher situations, but on ground that is still very wet, are *Leucobryum glaucum*, *Climacium americanum*, and *Thuidium delicatulum*. With the exception of *Leucobryum*, these species are also found on logs and sticks. *Anomodon rostratus* comes in where there is less moisture, particularly about tree bases. Here, as in the other mesophytic moss habitats, the soft hygroscopic mass of moss tissue forms a favorable place for the germination of tree seedlings and the seeds of other plants. As one approaches the higher land adjoining the sand dune to the north, the moss growth becomes less in quantity, but does not change very much in species until the dune itself is reached.

In the Hillside bog, a large part of which has reached the shrub stage, but in which there is much less water than at Mineral Springs, *Sphagnum recurvum* has been, and in places still is, the dominant vegetation. It must have reached a very luxuriant development in the recent past, but is now on the decline. In many places *Aulacomnium palustre* forms a second moss stage growing on *Sphagnum*, and this is frequently accompanied by *Polytrichum commune*. COOPER describes such an association in the *Sphagnum* bogs on Isle Royale. The bog itself has not yet developed the tree association, although with respect to moisture conditions it has advanced much beyond the bog at Mineral Springs. It is surrounded by climax beech-maple forest, and it is quite likely that this will be the fate of the bog if left to nature's influence. In the adjoining beech-maple forest *Catharinea undulata* is again the only moss of any prominence.

Table II represents the hydrarch succession from open water of lagoons and ponds to the climax forest. Once more the great importance of pioneer mosses in the advancement of the higher plant associations is shown. The economic value of shallow ponds is slight; while on the other hand they may be very injurious in that they harbor larvae of insects, harmful to man, so that the

elimination of such swampy regions may be very desirable. By the filling up of depressions the area may be made productive either as prairie or forest. The poorly drained deeper ponds are probably as little to be desired from an economic standpoint, since the water will not support the life of aquatic animals of commercial value. Consequently any natural agency which will further the change from hydrophytic to mesophytic conditions will add to the number of acres of productive land reclaimed from a state of total non-productivity, and also lead to better health conditions for the inhabitants of the surrounding country.

TABLE II

PRESENCE OF MOSS SPECIES IN ASSOCIATIONS OF HYDRARCH SUCCESSION

Species	Open water	Sedge mat	Tamaracks	Swamp forest	Beech-maple
Amblystegium riparium..	P	.....	P	.....	.....
Anomodon rostratus.....	.....	.....	P	P	.....
Aulacomnium palustre...	.....	P	.....	P	.....
Brachythecium sirulare..	.....	P	P	P	.....
Campylium stellatum....	P	P	P	.....	.....
Campylium hispidulum..	.....	P	P	.....	.....
Calliergon cordifolium...	.....	P	P	P	.....
Climacium americanum..	.....	.....	P	P	.....
Catharinea undulata....	.....	.....	.....	P	P
Drepanocladus aduncus..	P	P	P	.....	.....
Drepanocladus fluitans...	P	P	.....	.....	.....
Dicranum scoparium....	.....	.....	P	P	.....
Entodon cladorrhizans...	.....	.....	P	P	.....
Leucobryum glaucum...	.....	.....	P	P	.....
Mnium cuspidatum.....	.....	.....	P	P	.....
Polytrichum commune...	.....	.....	P	P	.....
Rhodobryum roseum....	.....	.....	P	P	.....
Stereodon haldanianum..	.....	.....	P	P	.....
Thuidium delicatulum...	.....	.....	P	P	.....
Thuidium recognitum...	.....	.....	P	P	.....

The pannes about Miller are mostly of recent origin and are not within easy reach of other habitats of aquatic mosses. This may account for the fact that the few species are present. The mosses found growing in all of these ponds, so far as observed, propagate vegetatively only, or with very rare spore production, thus virtually prohibiting their spread into distant ponds except when carried by birds or other animals. As previously mentioned, these mosses must be able to make a good recovery after periods of desiccation, and must also be able to resist covering to some extent, as these pannes

are subject to occasional dry seasons and frequent deposit of sand. The presence of the mosses soon leads to accumulation of humus over the sandy bottom and initiates the growth of semihydrophytes.

In the lagoon region is a far more extensive pond area, both as to actual number of ponds and variation in ecological development, caused by depth and size as well as by age of the individual lagoons. The chance for transfer of mosses from one pond to another is much better; the variation in depth permits the growth both of floating and fixed species, while the greater age has allowed time for accumulation of more humus, which leads to the introduction of still other species, as well as perhaps a more luxuriant growth of all. With these conditions comes the rapid advance of the shrub and forest or prairie successions. In the swamp forest the moss flora becomes increasingly a dominant factor in humus accumulation as the ecological succession advances toward the climax, but begins to decline with the close approach of the beech-maple association. This appears to be a result both of competition with other ground flora and of the smaller supply of available water near the surface.

Very little work has been done in determining conditions for plant life in the bogs, but from the xerophytic structures of many bog plants, and the shallow root systems of the trees, COWLES concludes that, while moisture is plentiful, the chemical content of the water is such as to have a toxic effect upon the root development of plants, and to prevent absorption of water to a great extent. In other words, this is a physiologically xerophytic habitat for seed plants. It is not known how far this may influence the development of mosses; that it is not very injurious is proved by the great abundance of some species, such as *Sphagnum*. On the sedge mat the shade may be considerable when cat-tails are abundant, but the sun's rays reach the ground more directly than in the forest. The humidity near the ground is probably greater than among the trees, but evaporation at times is also much greater. The mosses occupy the small spaces around the roots of the fen plants and often cling closely to them, forming a packing between the stems, but there are no large masses. In some places there is a luxuriant growth of marsh forget-me-not and other species of

low growing seed plants which nearly smother out the mosses. The increase in shade and possibly other conditions in the late shrub stage and early tree association apparently are unfavorable for most of the old herbaceous species, and new ones have not taken their places, so that there are large areas unoccupied by such ground vegetation. As in the pine dune, so also here we may have toxicity produced by decay of conifer needles. This probably does not greatly retard the moss development, although it may account in part for the change in species. With herbaceous plants, on the other hand, it may result in almost total elimination. The rapid increase of quantity and number of species of moss in the early tree association, therefore, is directly related to these environmental conditions. The greater shade and lower temperature are both more favorable to moss growth, and added to these is the lack of competition with other plants.

As the tamaracks are replaced by deciduous trees, the mosses give place to herbaceous seed plants. The chemical condition of the subsoil changes, more humus accumulates, moisture and humidity decrease. The mosses now are crowded out of their former locations until, with few exceptions, they persist only on sticks, logs, and tree bases, and we find in their place many ferns and seed plants. Competition seems to be the great cause of the elimination. Some general conclusions regarding the pond and lake successions of mosses are as follows.

Very few mosses appear in the pannes, but those which are present are coarse and aid in filling up the depressions. The lagoons are favorable habitats for floating species, while other mosses are abundant along the margin. Both produce material which is added to the muck on the bottom and which provides nourishment for other plants. Still other species assist in the formation of floating islands. In the bogs a few species of semi-aquatic mosses appear in the early fen stage in considerable quantities. There is a slight decrease in quantity in the shrub stage. A marked increase in quantity and number of species is evident in the early tamarack association and continues until the tamaracks are replaced by deciduous trees, making the tamarack the dominant moss association. In the later deciduous association there is

a continuous decline in the moss flora until the climax beech-maple forest is reached. Competition with other plants seems to be the determining factor as the successions advance beyond the semi-hydrophytic.

Conclusions

1. In the successions on sand, mosses are most abundant, both in number of species and in total quantity in the stage; in which they first become very noticeable, the pine stage; and they decrease through the early oak stages to either the oak or the beech-maple climax.

2. In the swamp and bog successions the greatest dominance of mosses is found usually in the swamp or bog forest association, which may or may not directly precede the climax.

3. The mosses found in running spring water and in stagnant water are of different species, but nearly all belong to the same family, the Hypnaceae.

4. The succession on floodplains is unimportant because of constant deposit of sediment over the germinating mosses.

5. Mosses are among the highly important pioneer plants on bare rock surfaces, and continue abundant far into the forest association.

6. From an economic standpoint mosses are of the greatest value in several respects. They are soil formers and provide favorable habitats for germination of higher plants. They assist largely in forming the surface mat over deep lakes and in filling up shallow bodies of water. They may take part in building up rocklike substances, as tufa. They help to make up floating islands on which higher plants may grow. They conserve moisture, and give it up slowly, thus aiding in the prevention of disastrous floods in the surrounding regions. They prevent erosion of clay or sand surfaces.

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